# Productivity and nutrient cycling in taiga forest ecosystems

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This paper considers the productivity and nutrient cycling in examples of the major forest types in interior Alaska. These ecosystem properties are examined from the standpoint of the control exerted over them by soil temperature and forest-floor chemistry. We conclude that black spruce *Picea mariana* (Mill.) B.S.P. occupies the coldest, wettest sites which support tree growth in interior Alaska. Average seasonal heat sums (1132 ± 32 degree days (DD)) for all other forest types were significantly higher than those encountered for black spruce (640 ± 40 DD). In addition, black spruce ecosystems display the highest average seasonal forest-floor and mineral-soil moisture contents. Forest-floor chemistry interacts with soil temperature in black spruce to produce the most decay-resistant organic matter. In black spruce the material is characterized by the highest lignin content and widest C/N (44) and C/P (404) ratios. Across the range of forest types examined in this study, soil temperature is strongly related to net annual aboveground tree production and the annual tree requirement for N, P, K, Ca, and Mg. Forest floor C/N and C/P ratios are strongly related to annual tree N and P requirement and the C/N ratio to annual tree production. In all cases these controls act to produce, in black spruce, the smallest accumulation of tree biomass, standing crop of elements, annual production, and element requirement in aboveground tree components.

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Cet article fournit des exemples de la productivité et du cycle des éléments chez les principaux types forestiers de l'intérieur de l'Alaska. Il fait état du contrôle qu'exercent la température de sol et de la chimie de la couverture morte sur les écosystèmes examinés. Les auteurs concluent que *Picea mariana* (Mill.) B.S.P. occupe les stations les plus froides et les plus humides parmi celles qui supportent une végétation forestière, à l'intérieur de l'Alaska. La moyenne des sommes de chaleur saisonnières (1132 ± 32 degrés-jours, DD) pour les autres types forestiers sont significativement plus grandes que celles qui caractérisent *P. mariana* (640 ± 40 DD). Les écosystèmes de cette espèce présentent aussi les teneurs moyennes en humidité du sol minéral et de la couverture morte les plus élevées. La chimie de la couverture morte agit en interaction avec la température du sol pour fournir une matière organique très résistante à la décomposition. Le matériel est caractérisé par sa forte teneur en lignine et par des ratios C/N (44) et C/P (404) très élevés. La température du sol est fortement reliée à la production ligneuse annuelle et aux besoins en N, P, K, Ca et Mg des peuplements, au sein de la gamme de types forestiers examinés dans cette étude. Les ratios C/N et C/P de la couverture morte sont fortement reliés aux besoins annuels en N et P des peuplements, alors que le ratio C/N est relié à la production ligneuse annuelle. Dans tous les cas, ces contrôles agissent pour produire chez *P. mariana* la plus faible accumulation de biomasse ligneuse et de minéralomasse, la plus faible production annuelle et les plus faibles besoins annuels en éléments, parmi les peuplements étudiés.

[Traduit par le journal]

## Introduction

A combination of environmental factors unique to the taiga result in generally lower rates of primary production and nutrient cycling compared with temperate latitude forest ecosystems (Van Cleve and Alexander 1981; Cole and Rapp 1981). These factors include drastic seasonal fluctuations in day length and temperature, a short growing season, low soil temperature, and the occurrence of permafrost (Van Cleve and Alexander 1981). During summer months, the amount of sunlight received at the earth's surface approaches 22 h, while during the winter months less than 4 h of sunlight occurs. Warmest air temperatures approach 30°C in June and July but exceed −40°C in January and February. The growing season ranges from 65 to 90 days but frost may occur through the 1st week of June and after the beginning of August. Soil heat sums (degree days (DD), 0°C at 10 cm depth) range from approximately 480 DD on cold black spruce (*Picea mariana* (Mill.) B.S.P.) sites to between 1000 and 1300 DD on warmer aspen (*Populus tremuloides* Michx.) sites (Van Cleve *et al.* 1983).

Permafrost, requiring a mean annual temperature of −1°C or less, occurs in a discontinuous pattern in the

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Alaskan taiga. It is primarily encountered on poorly drained or north-slope locations. Permafrost is important from the nutrient cycling and primary production standpoints for the following reasons: (*i*) it is associated with cold soil temperatures resulting in reduced decomposer and plant root activity and lower rates of nutrient recycling; (*ii*) it restricts the volume of soil which is effective in system nutrient cycling; and (*iii*) it restricts the downward movement of elements by leaching and hence their loss from the soil, except where soil solution may move downslope over the permafrost table.

From the standpoint of their soil association, the range of these factors across the taiga landscape is modified by the state factors topography, parent material, time, and biotic conditions reflected primarily in forest-floor accumulation (Jenny 1941, 1980). Topography is important in that north aspects and level sites receive less solar radiation than south aspects and therefore tend to be cooler. In addition, lowland, level sites may be poorly drained, associated with permafrost and its ramifications for nutrient cycling. On the other hand, shallow soils on steeper south-facing slopes display moisture deficits and exhibit plant community and soil properties (caliche) characteristic of semiarid regions (Van Cleve *et al.* 1983; Viereck *et al.* 1983). In the latter case productivity and nutrient cycling may suffer from moisture deficits. Ridge-top soils are also generally shallow over bedrock (Rieger *et al.* 1963), and may experience reduced moisture storage and higher element leaching compared with deeper, south-aspect, and permafrost-dominated soil.

Parent material provides the medium (soil) which physically and chemically supports system nutrient cycling. In interior Alaska, parent material interacts in a unique manner with topography to control soil drainage and, in turn, forest productivity and nutrient cycling. For example, lowland soils developing in sandy-textured parent material and underlain by gravel tend to be well drained and support productive white spruce and balsam poplar (*Populus balsamifera* L.) forests. However, lowland soil developing in fine-textured material may be poorly drained, underlain by permafrost, and support low productivity black spruce ecosystems (Viereck 1970; Van Cleve and Viereck 1981).

Time is important from the standpoint that the succession of forest types encountered in lowland and upland ecosystems is associated with gradual accumulation of forest-floor organic matter. This occurs up to a maximum which approaches 10 kg/m$^2$ in black spruce ecosystems (Van Cleve and Viereck 1981). Associated with this phenomenon is a reduction in soil temperature and the reappearance of permafrost, or the development of shallower active layers on soils in which permafrost already exists (Heilman 1968; Viereck 1970).

These phenomena contribute to the mosaic pattern of forest types and to the range of productivity and nutrient cycling observed in the Alaskan taiga. The objective of the present paper is to provide a test of the forest productivity and nutrient cycling aspects of the central hypothesis of the taiga research program. Specifically, these properties of forest ecosystems are largely controlled by cold soil temperature. We evaluate the production and nutrient dynamics of black spruce ecosystems in comparison with other major forest types which comprise the mosaic of taiga vegetation in interior Alaska.

## Field and laboratory methods

Sites selected for analysis of productivity and nutrient dynamics are described by Viereck *et al.* (1983). They encompass much of the range of conditions representative of ecosystem state and function encountered in the Alaskan taiga. A list of variables measured at the respective sites is presented in Table 1. While tree-root and shrub biomass were determined for a number of these sites, the picture is incomplete. The broadest range of information deals with aboveground tree standing crop of biomass and selected chemical elements (N, P, K, Ca, Mg), annual tree production, and element requirement. Field-sampling procedures for estimating these parameters are described in Van Cleve *et al.* (1981). Estimates of production and element requirement were obtained as close to the peak tree growth season as possible.

Procedures for sampling litter fall and mineral soil are described in Viereck *et al.* (1983). The forest floor was sampled at each site from four randomly located 1-m$^2$ quadrats. From the opposite quarters of each quadrat, two 15-cm-diameter cores of mineral soil were removed. In white and black spruce stands the 01, 021, and 022 horizons (collected within each square metre) were separately pooled. In birch, aspen, and poplar stands, the 01 horizon for the entire square metre was separately collected for each quadrat. Then, two 15-cm-diameter cores were obtained and the 021 and 022 horizons pooled for each square metre as previously described. The *n*-value for each horizon and forest type was 4.

Throughfall was measured in birch (*Betula papyrifera* Marsh., stand 16), aspen (stand 15), and black spruce (stands 33, 34, and 19). Six collectors each were randomly located in the birch, aspen, and stand 19 black spruce. Along each of two transects at sites 33 and 34, nine sampling points were uniformly spaced at 20-m intervals. At each point, one throughfall collector was randomly located within 5 m of the transect. Collectors consisted of 3-L polyethylene jars fitted with 28-cm-diameter polyethylene funnels. The funnels contained a loose plug of Pyrex glass wool to prevent coarse and fine particulate material from entering the collecting reservoir. The glass wool was replaced as needed.

Observations of black and white spruce (*Picea glauca* (Moench) Voss) showed essentially no stemflow in these forest types. Substantial amounts of stemflow were encountered in birch and aspen. This flux of nutrients was measured using foam collars (Likens and Eaton 1970) attached to 14 trees in the aspen (stand 15) and 12 trees in the birch (stand 16) forests. Diameter breast height of the trees spanned the range

TABLE 1. Selected characteristics and variables measured at respective study sites

| Vegetation type | Stand No. | Age | Topographic aspect/slope | Location elevation (m) | Overstory | Shrubs | Moss | Forest floor | Mineral soil | Litter fall | Throughfall | Stemflow | Soil solution |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Black spruce | 14 | 145 | N 30% | 427 | — | — | — | P, T | P | F | — | — | — |
| | 21 | 60 | NW 15% | 470 | P, Pr, R | P | P | P, T | P | F | — | — | F |
| | 33,34 | 130 | SE 10% | 390 | P, Pr, R | P, P, R | P | P, T | P | F | F | — | F |
| | 19 | 130 | NW 2% | 343 | P, Pr, R | P | P | P, T | P | F | F | — | F |
| | 20 | 60 | 0 | 167 | P, Pr, R | P | P | P, T | P | F | — | — | — |
| | 18 | 70 | 0 | 468 | — | — | — | P | P | F | — | — | — |
| | 29 | 130 | 0 | 177 | — | — | — | P | P | F | — | — | — |
| | 30 | 150 | 0 | 122 | — | — | — | P | P | F | — | — | — |
| White spruce | 12 | 165 | S 25% | 396 | P, Pr, R | — | — | P, T | P | F | — | — | — |
| | 22 | 70 | SE 18% | 229 | — | — | — | P, T | P | F | — | — | F |
| | 26 | 115 | 0 | 185 | P, Pr, R | — | — | P, T | P | F | — | — | — |
| | 27 | 130 | 0 | 177 | — | — | — | P | P | F | — | — | — |
| | — | 55 | 0 | 185 | P, Pr, R | — | — | — | — | — | — | — | — |
| | — | 180 | 0 | 185 | P, Pr, R | — | — | — | — | — | — | — | — |
| | 31 | 250 | 0 | 185 | — | — | — | P, T | P | F | — | — | — |
| Paper birch | 13 | 130 | E 32% | 381 | P, Pr, R | — | — | P, T | P | F | — | — | — |
| | 16 | 60 | S 15% | 229 | P, Pr, R | P | — | P, T | P | F | F | F | F |
| | — | 44 | NW 15% | 396 | P, Pr, R | — | — | — | — | — | — | — | — |
| Quaking aspen | 11 | 50 | SE 75% | 182 | P, Pr, R | — | — | P, T | P | F | — | — | — |
| | 15 | 60 | S 15% | 229 | P, Pr, R | P | — | P, T | P | F | F | F | F |
| | — | 45 | 0 | 198 | — | — | — | P | P | F | — | — | — |
| Balsam poplar | 24 | 100 | 0 | 122 | P, Pr, R | — | — | P, T | P | F | — | — | — |
| | 25 | 60 | 0 | 177 | P, Pr, R | — | — | P, T | P | F | — | — | — |
| | 32 | 50 | 0 | 120 | P, Pr, R | — | — | P, T | P | F | — | — | — |

NOTE: P, pool size of biomass and nutrients; Pr, annual production; R, annual element requirement; T, turnover of organic matter and nutrients; F, element content in this system flow; in case of litter fall also includes biomass.

of diameters encountered in each stand. Stemflow was collected in 18-L polyethylene containers attached to each tree.

Soil solution was collected using 27-cm-diameter, 0.5-bar (1 bar = 100 kPa) ceramic plates and methods were described by Cole (1968). Four plates were randomly installed beneath the forest floor in each vegetation type and suction was maintained at 10 ± 0.1 kPa. Leachate was collected in 18-L Pyrex glass containers.

Throughfall, stemflow, and soil-solution samples were collected weekly. Unless immediately processed all water samples were frozen until analyzed. The same analytical methods generally were employed for all water samples. Acidity was determined using a radiometer PHM64 glass electrode pH meter. Concentration of K, Ca, and Mg was estimated using a Perkin–Elmer model 305B and later model 5000 atomic absorption spectrophotometer. Kjeldahl nitrogen (including $NH_4$ N) was determined according to methods of Bremner (1965). Ammonium, nitrate, and phosphate were estimated using an autoanalyzer and methods outlined by Technicon (Whitledge *et al.* 1981).

Methods employed for chemical analysis of plant tissue and mineral soil are described by Van Cleve *et al.* (1981) and Van Cleve and Viereck (1972).

*Calculations*

Methods employed in calculating the standing stock of biomass and chemical elements, annual production, and element requirement on a unit area basis are described in Van Cleve *et al.* (1981). All of these estimates and those of pool sizes of organic matter and element content of the forest floor, mineral soil, and litter fall are expressed on an ovendry weight basis.

Element contents of stemflow were expressed on a unit area basis by comparison of the basal area of sample trees with stand basal area. Sample tree diameter distribution was the same as that for the stand. Soil-solution element contents were adjusted to the unit area basis according to the volume of solution passing through the average surface area of the plate employed (573 $cm^2$).

All ecosystem stand and element flux estimates are expressed as weight per square metre. In the case of stands where throughfall or stemflow data were not available these parameters were separately estimated on an annual basis as a portion of annual litter fall since this variable was measured in nearly all stands. For balsam poplar, aspen, and birch stands, throughfall and stemflow were estimated as fractions of litter fall based on the average of ratios determined for these fluxes in stands 15 (aspen) and 16 (birch). For white and black spruce stands throughfall was estimated on the basis of the average of ratios for this parameter determined in black spruce stands 33, 34, and 19. While these estimates are not as reliable as those obtained directly from the respective stands, they provide an approximation of these fluxes from vegetation types which are generally related in leaf morphology.

Terminology with regard to elemental uptake, requirement, return, and recycling by the tree overstory follows that outlined by Cole and Rapp (1981). Elemental uptake is defined as the annual increment associated with bole and branch wood plus annual loss through litter fall, leaf wash, and stemflow. A steady state is assumed for tree foliage and no consideration is given to root or bark increment. Elemental requirement is defined as the annual element increment associated with bole and branch wood and tree foliage. The same assumptions apply to this calculation as were considered for uptake.

Appendix tables[2] summarize environmental parameters and selected ecosystem state and flux variables using the format of Cole and Rapp (1981). Less than a 5-year period has passed during which climatic records were obtained at many of the semi-intensive sites. Therefore, the precipitation, temperature, and length of growing season estimates are only for the general Fairbanks area. Mineral-soil profiles were sampled to bedrock, permafrost or a maximum depth of 70 cm.

## Results and discussion

*Standing crop of biomass and nutrients*

Accumulation of biomass and chemical elements in taiga forests primarily reflects the unique combination of state factors (Jenny 1941, 1980), especially soil temperature, which characterize the biome. In this study, mature site types were examined for production and nutrient dynamics. These included stands of moderate age (45–60 years) in all major forest types (Table 1). However, the average age of the types generally was older for white (134 years) and black (95 years) spruce compared with aspen (55 years), birch (77 years), and poplar (70 years, Fig. 1). With regard to the more productive vegetation type, this condition undoubtedly reflected the relatively earlier successional position of poplar, birch, and aspen compared with white spruce in floodplains in south-aspect successional sequences (Van Cleve and Viereck 1981). Black spruce generally has greater longevity than birch, aspen, or poplar and comprises the climax forest type on floodplains in the interior of Alaska (Viereck 1970). In the uplands, black spruce stands may exceed 200 years in age (Van Cleve and Viereck 1981).

The accumulated tree biomass and standing crop of N and K, averaged across the more productive forest types (white spruce, aspen, birch, and poplar) were between 2 and 4 times higher than encountered in black spruce (Fig. 1, Table 2). Amounts of P, Ca, and Mg also were 2 to 3 times greater than found in black spruce although the differences between the two groups of forest types were not statistically significant.

Largest average accumulation of aboveground tree biomass was encountered in white spruce. The total at 134 years, 17.4 $kg/m^2$, is more than 3 times the 5.1 $kg/m^2$ accumulated in black spruce (Table 2, Fig. 1). For stands of approximately 165 and 130 years the total tree biomass is 25 and 8 $kg/m^2$ for white and black spruce, respectively. On the average, approximately twice the standing tree biomass was encountered in

[2]Appendix tables are available from: Depository of Unpublished Data, Canada Institute for Scientific and Technological Information, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

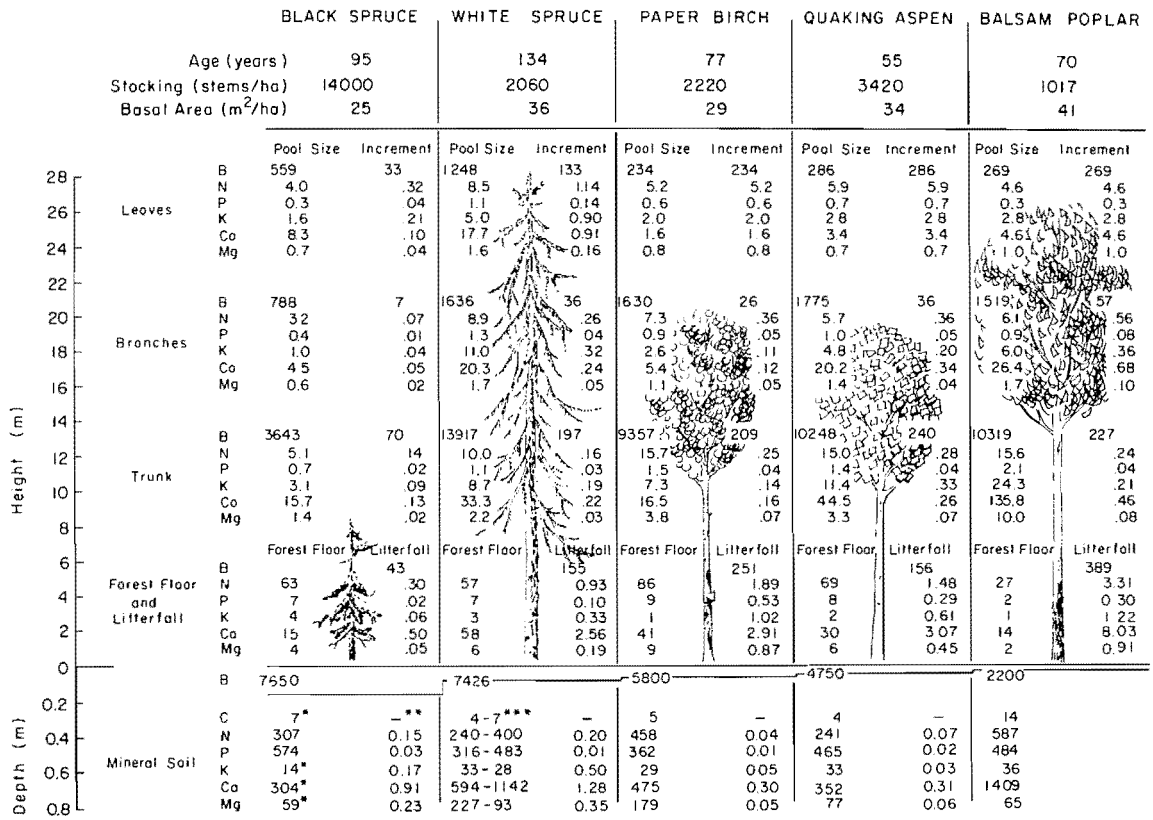


FIG. 1. Distribution and flux of selected elements in principal taiga forest types of interior Alaska, values in grams per square metre unless noted. (*) Carbon in kilograms per square metre, base elements estimated from ion exchange analysis, N and P are Kjeldahl and total P analysis. (**) Estimates of soil solution flow through the rooting zone. (***) In the case of white spruce mineral soil, left-hand figures are for uplands, right-hand figures are for floodplains. All values in figure are average of all stands sampled within a forest type. Height of trees and depth of forest floor in respective types are drawn to scale.

hardwood (aspen, birch, poplar) stands, 11 to 12 kg/m$^2$, compared with the black spruce, despite the younger age of the hardwood stands. This generally reflects a smaller mass of organic matter in each compartment (leaves, branches, trunk) in black spruce compared with the other forest types. The greater leaf longevity of the spruces is emphasized by the fact that on the average a significantly larger portion, 11% or 903 g/m$^2$, of their tree biomass comprises foliage while foliage constitutes only 3% of hardwood tree biomass.

The average tree standing crop of N and P in white spruce and the hardwoods (25−28 g/m$^2$ and 2.7−3.2 g/m$^2$, respectively; Fig. 1, Table 2) may reflect the high demand of aspen, birch, and poplar for these elements per unit of production. These averages are approximately twice the N but only 1.6 times the P accumulated by black spruce. On the average, the coniferous types accumulate a significantly larger portion (33 to 34%) of aboveground P and N in foliage compared with 19 and 22% in the hardwood types, due primarily to their large biomass allocation to leaves. Black spruce generally shows the smallest average foliage mass of N and P. In the case of P the amounts are equal to those encountered in poplar, 0.3 g/m$^2$ (Fig. 1). This condition may reflect the high mineral soil Ca concentrations which exist in floodplain balsam poplar soils compared with other taiga forest soil and indicate interference with translocation of P to leaves. Average estimates show poplar tree branches and trunks to have the highest Ca concentrations (Fig. 1).

With the exception of Ca, average base element (K, Ca, Mg) accumulation in aboveground tree parts generally is lowest in black spruce. Calcium accumulation was found to be lowest in paper birch, 22 g/m$^2$, compared with 28 g/m$^2$ in black spruce (Table 2). Sixty-five to 67 g/m$^2$ accumulated aboveground in aspen and white spruce, respectively, but the maximum average of 155 g/m$^2$ was encountered in poplar. For K, aboveground tree totals averaged 12 to 33 g/m$^2$ in the more productive forest types and 6 g/m$^2$ in black spruce. A

TABLE 2. Comparison of standing crop of biomass and mass of selected elements in aboveground tree components ($\bar{x} \pm$ SE, grams per square metre)

| | | Biomass | | N | | P | | K | | Ca | | Mg | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vegetation type | $n$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ |
| Black spruce | 4 | 2589–10984 | 5094±2107 | 3.9–21.0 | 12.2±3.6 | 0.51–3.88 | 1.82±0.72 | 2.47–7.38 | 5.89±1.63 | 7.4–64.7 | 28.1±13.0 | 0.71–6.23 | 2.71±1.28 |
| White spruce | 4 | 6152–24577 | 17442±4279 | 8.7–31.9 | 25.0±5.5 | 1.15–5.83 | 3.10±0.98 | 7.58–37.92 | 23.05±3.10 | 32.6–97.7 | 67.2±13.4 | 1.90–7.08 | 4.51±1.50 |
| Quaking aspen | 2 | 4653–17490 | 11021±6419 | 12.8–38.1 | 25.9±12.3 | 1.67–3.75 | 2.71±1.04 | 9.98–26.21 | 18.10±8.10 | 38.4–92.2 | 65.3±26.9 | 1.82–8.46 | 5.14±3.32 |
| Paper birch | 3 | 9192–14713 | 11156±1782 | 20.9–36.5 | 27.5±4.7 | 1.65–4.08 | 2.86±0.70 | 8.76–16.52 | 11.75±2.41 | 14.2–32.0 | 21.8±5.3 | 3.86–9.58 | 5.60±1.99 |
| Balsam poplar | 3 | 4067–18027 | 12097±4165 | 8.1–36.0 | 26.0±9.0 | 1.04–5.01 | 3.24±1.17 | 10.47–46.17 | 32.88±11.30 | 4.2–345.5 | 154.5±100.6 | 3.62–22.02 | 12.60±5.32 |
| White spruce, aspen, birch, poplar | 12 | | 13473±1990* | | 26.7±3.1* | | 3.01±0.44 | | 21.86±3.99* | | 77.3±26.5 | | 7.01±1.64 |

*Mean significantly different from mean for black spruce at $\alpha = 0.05$.

TABLE 3. Range and average annual biomass production and requirement for selected elements in aboveground tree components ($\bar{x} \pm$ SE, grams per square metre)

| | | Biomass | | N | | P | | K | | Ca | | Mg | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vegetation type | $n$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ |
| Black spruce | 4 | 72–148 | 113±17 | 0.29–0.82 | 0.51±0.11 | 0.02–0.12 | 0.07±0.02 | 0.17–0.47 | 0.32±0.07 | 0.17–0.38 | 0.26±0.05 | 0.04–0.09 | 0.07±0.01 |
| White spruce | 4 | 238–540 | 366±63 | 0.74–2.77 | 1.56±0.43 | 0.13–0.24 | 0.20±0.03 | 0.66–2.43 | 1.41±0.41 | 1.07–1.87 | 1.37±0.17 | 0.15–0.32 | 0.24±0.03 |
| Quaking aspen | 2 | 363–760 | 565±199 | 4.02–8.25 | 6.14±2.12 | 0.47–1.00 | 0.74±0.27 | 2.38–3.96 | 3.17±0.79 | 2.36–5.54 | 3.95±1.59 | 0.29–1.24 | 0.77±0.48 |
| Paper birch | 3 | 343–572 | 470±61 | 5.37–6.43 | 5.85±0.31 | 0.60–0.72 | 0.72±0.07 | 1.64–2.59 | 2.24±0.30 | 1.87–1.88 | 1.87±0.00 | 0.81–1.03 | 0.91±0.06 |
| Balsam poplar | 3 | 264–952 | 552±206 | 2.86–8.24 | 5.55±2.69 | 0.24–0.68 | 0.41±0.14 | 2.42–4.87 | 3.34±0.77 | 3.86–8.09 | 5.72±1.25 | 0.82–1.46 | 1.17±0.19 |

range of 5 to 13 g/m$^2$ of Mg was found in white spruce, aspen, birch, and poplar but only 3 g/m$^2$ accumulated in black spruce. Consistently larger portions of the base elements were associated with foliage in the coniferous forest types. These totals ranged from 22 to 28%, 26 to 30%, and 25 to 34% for K, Ca, and Mg, respectively, in the spruces compared with 8 to 17%, 3 to 7%, and 8 to 14% for K, Ca, and Mg, respectively, in the hardwoods.

For N, P, and the base elements, larger nutrient accumulations were encountered in trunk wood plus bark of aspen, birch, and poplar compared with white and black spruce. Consistent trends were not observed between black and white spruce.

*Annual biomass increment and element requirement*

Among the productive forest types, average annual aboveground tree biomass production ranged from 366 g/m$^2$ in white spruce to 562 g/m$^2$ in aspen (Fig. 1, Table 3). Paper birch (470 g/m$^2$) and poplar (522 g/m$^2$) production fell between these extremes. Production in these vegetation types ranged from 3 to 5 times higher than that encountered in black spruce (113 g/m$^2$). The highest annual biomass production, 952 g/m$^2$, estimated for a 60-year-old balsam poplar forest, was approximately 13 times greater than the lowest production, 72 g/m$^2$, measured in a 57-year-old black spruce forest.

Average annual requirement of N, P, and K ranged from 3 to 10 times greater in white spruce, aspen, birch, and poplar than in black spruce (Table 3). Among the productive forest types, minimum requirement for these elements, 1.56 g/m$^2$ (N), 0.20 g/m$^2$ (P), and 1.41 g/m$^2$ (K) were displayed by white spruce. Two to 4 times greater requirement for these nutrients was exhibited by the hardwood types compared with white spruce. Average annual black spruce requirement, lowest of the five forest types, ranged from 0.07 g/m$^2$ for P to 0.32 and 0.51 g/m$^2$ for K and N, respectively. Extreme differences in requirement between black spruce and the productive forest types approached 30-fold for these nutrients (Table 3). Compared with the low black spruce requirement, maximum values among the hardwood types were 5.6 to 6.1 g/m$^2$ for N, 0.40 to 0.74 g/m$^2$ for P, and 2.4 to 4.9 g/m$^2$ for K.

White spruce showed a 3 to 5 times larger average annual requirement for Mg and Ca, respectively, than did black spruce. Maximum average requirement for Mg (1.17 g/m$^2$) and Ca (5.72 g/m$^2$) was encountered in poplar. At the extreme, the most productive poplar stand required nearly 50 times more Ca (8.1 g/m$^2$) and 40 times more Mg (1.5 g/m$^2$) than did the least productive black spruce forest.

The annual tree production and element requirement averaged across the more productive forest types (white spruce, aspen, birch, poplar) is significantly greater

TABLE 4. Comparison of annual biomass production and requirement for selected elements in aboveground tree components ($\bar{x} \pm$ SE, grams per square metre) and efficiency of element use ($\bar{x} \pm$ SE, biomass production/element requirement)

| Vegetation type | $n$ | Biomass production | N | | P | | K | | Ca | | Mg | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Requirement | Efficiency | Requirement | Efficiency | Requirement | Efficiency | Requirement | Efficiency | Requirement | Efficiency |
| *(A) Black spruce compared with all other forest types* | | | | | | | | | | | | |
| Black spruce | 4 | 113.2±16.8 | 0.51±0.10 | | 0.068±0.02 | | 0.32±0.07 | | 0.26±0.05 | | 0.07±0.01 | |
| White spruce, birch, aspen, poplar | 12 | 461.7±65.9** | 4.29±0.82* | | 0.470±0.08* | | 2.39±0.34** | | 3.01±0.64* | | 0.73±0.13† | |
| *(B) Coniferous type compared with deciduous broadleaved forest types* | | | | | | | | | | | | |
| White spruce, black spruce | | 239.4±56.4 | 1.04±0.29 | 245±18 | 0.130±0.03 | 1921±225 | 0.86±0.28 | 343±47 | 0.81±0.23 | 347±40 | 0.15±0.04 | 1686±87 |
| Birch, aspen, poplar | | 523.6±81.8* | 5.85±0.71** | 89±5** | 0.610±0.09** | 936±124** | 2.89±0.36 | 180±13** | 3.83±0.81** | 164±30** | 0.97±0.13** | 591±104** |

*, **Difference between means significant at $\alpha = 0.05$, $\alpha = 0.01$, respectively.

TABLE 5. Average nutrient efficiency for respective vegetation types (net annual production/net annual element requirement, $\bar{x} \pm$ SE)

| Vegetation type | $n$ | N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|
| Black spruce | 4 | 232±23 | 2005±425 | 383±78 | 430±52 | 1825±134 |
| White spruce | 4 | 257±30 | 1837±226 | 303±58 | 263±17 | 1547±57 |
| Quaking aspen | 2 | 91±1 | 767±7 | 173±20 | 146±9 | 933±320 |
| Paper birch | 3 | 80±8 | 663±101 | 210±11 | 251±36 | 511±44 |
| Balsam poplar | 3 | 98±9 | 1322±113 | 155±25 | 90±15 | 433±105 |

than that encountered in black spruce. The average requirement ranged from an order of magnitude larger for Ca (0.26 vs. 3.01 g/m$^2$) and Mg (0.07 vs. 0.73 g/m$^2$) to between 7 and 8 times greater for N, P, and K (Table 4A). Annual production is approximately 4 times higher (462 g/m$^2$) compared with black spruce (113 g/m$^2$).

The broadleaved, deciduous forest types (hardwoods) show an average production approximately twice that of the coniferous types (524 g/m$^2$ vs. 239 g/m$^2$, Table 4B). Element requirement also is generally greater for these types compared with coniferous stands, ranging from threefold higher for K to sevenfold higher for Mg. However, on the average, the efficiency of element use (annual production/annual element requirement) is 2 to 3 times greater in black and white spruce compared with the hardwood types (Table 4B). There is no marked difference in element efficiency between black and white spruce (Table 5). This condition holds for K among the hardwoods. Among these types more substantial differences are encountered for the other elements.

*Litter fall and element flows in water-related pathways*

The markedly greater return of biomass and nutrients with litter fall in white spruce and the hardwood types emphasized the higher productivity and more dynamic nature of nutrient cycling in these productive forests compared with black spruce (Fig. 1, Tables 6 and 7). From 4 to 9 times more organic matter was returned to the forest floor in litter fall in the more productive forests compared with black spruce (Table 6). The average returns ranged from about 155 g/m$^2$ in white spruce and aspen to 390 g/m$^2$ in poplar. An average of 43 g/m$^2$ is returned in black spruce. In black spruce, the average annual return of N (0.3 g/m$^2$), P (0.02 g/m$^2$), K (0.06 g/m$^2$), Ca (0.5 g/m$^2$), and Mg (0.05 g/m$^2$), constitutes a 10- to 20-fold smaller flux than in white spruce. Average maximum return for N (3.31 g/m$^2$) and Ca (7.81 g/m$^2$) was found in poplar, P (0.53 g/m$^2$) in birch, and Mg (0.87 g/m$^2$) in birch and poplar (Table 6). On the average the hardwood stands return 3 times the biomass (290 vs. 91 g/m$^2$) and from 4 to 8 times the mass of elements than are returned in the coniferous forest types (Table 7).

In black spruce ecosystems, litter fall may comprise a three to fourfold larger flow of P and Ca than throughfall on an annual basis. The flow ranges between 0.01 and 0.23 g/m$^2$ for these elements (Table 8). However, more K and Mg are returned to the forest floor in throughfall than in litter fall. These two fluxes contain approximately equal amounts of N. Phosphorus consistently is present in smallest amounts in throughfall compared with the other elements (0.01 g/m$^2$). With the exception of N and K, leaching through the rooting zone consistently is equal to or larger than the flux in throughfall (up to 6 times larger for Mg).

In birch and aspen ecosystems, element flux in litter fall consistently comprises the largest of all types of nutrient flows (Table 8). The difference is more than an order of magnitude greater than leaching loss for all elements and the same magnitude of difference for P, Ca, and Mg in throughfall and stemflow. In comparison, nutrient flows in the water-related pathways were approximately half that in litter fall in Illinois oak–hickory forests (Rolfe *et al.* 1978). Generally larger flow in throughfall and stemflow was found in aspen than black spruce forests in north central Minnesota (Verry and Timmons 1977). In the latter case largest flux was encountered for K and Ca (1.52 and 1.47 g/m$^2$, respectively) in aspen and N and Ca (0.63 and 0.48 g/m$^2$, respectively) in black spruce. These amounts are 2 to 5 times and 2 to 3 times larger, respectively, than flows of these elements in taiga aspen and black spruce forests. The differences largely reflect the nearly threefold greater annual precipitation encountered in the Minnesota study area (775 mm) compared with the Alaskan study area (286 mm).

Black spruce ecosystems have buffering compartments and mechanisms which tend to conserve site nutrient capital. Thick forest-floor organic layers accumulate which have slow mineralization rates and high cation exchange capacities. These layers insulate the soil, maintaining cool soil temperatures, reducing mineral-soil microbial activity, and maintaining the thermal integrity of permafrost and hence overall site stability. In turn, permafrost acts as a sink for nutrient elements. Black spruce is the slowest growing forest tree in interior Alaska, retaining its foliage for up to 25

TABLE 6. Litter-fall biomass and nutrient content for selected taiga forest types ($\bar{x}$ ± SE, grams per square metre)

| | | Biomass | | N | | P | | K | | Ca | | Mg | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vegetation type | *n* | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ |
| Black spruce | 8 | 15–142 | 43.1±11.4 | 0.07–0.94 | 0.30±0.10 | 0.01–0.09 | 0.02±0.01 | 0.02–0.26 | 0.06±0.02 | 0.17–1.90 | 0.50±0.16 | 0.01–0.34 | 0.05±0.03 |
| White spruce | 4 | 95–316 | 155.0±77.5 | 0.54–2.01 | 0.93±0.28 | 0.05–0.20 | 0.10±0.02 | 0.11–0.76 | 0.33±0.08 | 1.59–6.10 | 2.56±0.77 | 0.08–0.44 | 0.19±0.06 |
| Quaking aspen | 3 | 27–222 | 156.0±65.0 | 0.28–2.23 | 1.48±0.61 | 0.04–0.48 | 0.29±0.13 | 0.26–0.96 | 0.61±0.20 | 0.39–4.80 | 3.07±1.36 | 0.05–0.68 | 0.45±0.20 |
| Paper birch | 4 | 233–265 | 251.0±7.7 | 1.38–2.56 | 1.89±0.25 | 0.50–0.57 | 0.53±0.02 | 0.83–1.38 | 1.02±0.13 | 2.08–3.45 | 2.91±0.30 | 0.81–0.92 | 0.87±0.02 |
| Balsam poplar | 3 | 268–653 | 389.0±49.0 | 2.16–6.66 | 3.31±0.74 | 0.15–0.45 | 0.30±0.06 | 0.56–2.39 | 1.32±0.35 | 5.67–11.78 | 8.03±0.91 | 0.73–1.25 | 0.91±0.18 |



TABLE 7. Comparison of biomass and element return in litter fall for selected forest types ($x$ ± SE, grams per square metre)

| Vegetation type | *n* | Biomass | N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|---|
| Black spruce | 8 | 43.1±11.4 | 0.298±0.098 | 0.023±0.007 | 0.056±0.018 | 0.500±0.159 | 0.054±0.029 |
| White spruce, aspen, birch, poplar | 14 | 246.2±26.3** | 1.897±0.281** | 0.318±0.050** | 0.808±0.132** | 4.156±0.644** | 0.612±0.093** |
| Black spruce, white spruce | 13 | 90.7±21.3 | 0.578±0.145 | 0.055±0.014 | 0.164±0.046 | 1.358±0.395 | 0.115±0.033 |
| Birch, aspen, poplar | 9 | 290.3±28.9** | 2.380±0.320** | 0.435±0.039** | 1.017±0.137** | 4.947±0.850** | 0.833±0.063** |

**Means significantly different at $\alpha = 0.01$.

TABLE 8. Comparison of mean annual element flows in litter fall and water related pathways (grams per square metre)

| Vegetation type | Parameter | Stand No. | N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|---|
| Black spruce | P | 19 | 0.23 | 0.007 | 0.16 | 0.39 | 0.11 |
| | T | | 0.35 | 0.010 | 0.22 | 0.13 | 0.29 |
| | L | | 0.36 | 0.040 | 0.07 | 0.41 | 0.03 |
| | Le | | 0.19 | 0.020 | 0.15 | 0.86 | 0.26 |
| | D | | +0.04 | −0.013 | +0.01 | −0.47 | −0.15 |
| Black spruce | P | 33,34 | 0.16 | 0.005 | 0.10 | 0.28 | 0.04 |
| | T | | 0.19 | 0.005 | 0.13 | 0.23 | 0.04 |
| | L | | 0.15 | 0.010 | 0.03 | 0.35 | 0.02 |
| | Le | | 0.17 | 0.020 | 0.19 | 1.27 | 0.24 |
| | D | | −0.01 | −0.015 | −0.09 | −0.99 | −0.20 |
| Paper birch | P | 16 | 0.21 | 0.006 | 0.05 | 0.08 | 0.01 |
| | T + S | | 0.32 | 0.031 | 0.33 | 0.17 | 0.06 |
| | L | | 1.80 | 0.500 | 0.83 | 3.45 | 0.92 |
| | Le | | 0.04 | 0.010 | 0.05 | 0.30 | 0.05 |
| | D | | +0.17 | −0.004 | 0 | −0.22 | −0.04 |
| Quaking aspen | P | 15 | 0.21 | 0.006 | 0.05 | 0.08 | 0.01 |
| | T + S | | 0.35 | 0.022 | 0.33 | 0.67 | 0.09 |
| | L | | 2.23 | 0.480 | 0.96 | 4.80 | 0.68 |
| | Le | | 0.07 | 0.020 | 0.03 | 0.31 | 0.06 |
| | D | | +0.14 | −0.014 | +0.02 | −0.23 | −0.05 |

P, precipitation; T, throughfall; S, stemflow; L, litter fall; Le, leaching; D, deficit or precipitation−leaching; +, gain; −, loss for ecosystem.

years in some cases. Hence energy, nutrient demands, and growth are much reduced compared with birch, aspen, and poplar. The average relative growth rates in black spruce, 0.02 net annual production per gram of standing biomass, is approximately 40 to 50% of that encountered in the broadleaved deciduous vegetation types (0.04 to 0.05 g/g).

It is surprising then that substantial amounts of some elements, compared with the annual element requirement (Table 3), may be leached through the rooting zone and possibly lost to recycling in the ecosystem. Estimates of the seasonal volume of soil solution moving through the rooting zone show from 2 to 10 times (120 to 300 $L/m^2$) larger volume in black spruce than in birch (31 $L/m^2$) or aspen (59 $L/m^2$) forests. This condition is associated with between 2 and 5 times more N, K, Ca, and Mg moving below the rooting zone in black spruce than in the hardwood forest types. In the case of P the flux below the rooting zone is approximately equal regardless of vegetation types (Table 8).

In black spruce, the losses of N below the rooting zone are about equal to gains of N from precipitation. In aspen and birch ecosystems, the gains are approximately 3 and 5 times larger for N than flux below the rooting zone. In the case of P, Ca, and Mg, leaching removes between 2 and 6 times more nutrient than is added in precipitation. The relationship between gains and leaching losses is not consistent among forest types. A balance, or slight gain appears in birch and aspen while balance or loss exists in the permafrost-free and permafrost-dominated black spruce systems, respectively. However, on the basis of instantaneous element pool size analysis of the forest floor, these losses appear to be insignificant with regard to ecosystem function (Tables 9, 10, and 11). The total and exchangeable element estimates indicate that these pools are up to several orders of magnitude larger than deficits incurred by leaching. Larger elemental leaching losses in black spruce than in birch or aspen reflect generally higher soil moisture concentrations in black spruce (Fig. 2). This condition primarily is maintained by reduced evapotranspiration and poor soil drainage in black spruce ecosystems. Larger precipitation inputs of K, Ca, and Mg in black spruce are due to location of the study sites in the vicinity (1 to 2 mi or closer (1 mi = 1.609344 km)) of unpaved roads with resulting addition to precipitation in collectors of these elements even though procedures were adopted to avoid this difficulty.

*Forest-floor biomass and nutrient status*

Largest accumulated organic matter reserves on the forest floor generally were encountered in black spruce. An average of 7.6 $kg/m^2$ was determined for all these sites with a range of 4.5 to 9.2 $kg/m^2$ (Fig. 1, Tables 9 and 10A). In the other sites, the average forest-floor biomass ranged from 7.4 $kg/m^2$ (white spruce) to 2 $kg/m^2$ (balsam poplar). The latter, low value reflects periodic siltation of the forest floor in these floodplain

TABLE 9. Total pool size (grams per square metre) and concentration (percent) for selected elements in forest floor ($\bar{x} \pm$ SE)

| Vegetation type | $n$ | Biomass | % N | Mass N | % P | Mass P | % K | Mass K | % Ca | Mass Ca | % Mg | Mass Mg |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Black spruce | 8 | 7646±601.9 | 0.83±0.04 | 62.5±5.26 | 0.09±0.01 | 7.3±0.9 | 0.218±0.017 | 17.7±2.34 | 0.33±0.03 | 26.7±3.3 | 0.111±0.014 | 9.1±1.6 |
| White spruce | 4 | 7426±1496.0 | 0.85±0.06 | 57.2±5.30 | 0.10±0.01 | 6.5±0.7 | 0.450±0.110 | 34.7±18.30 | 1.33±0.11 | 92.1±30.8 | 0.400±0.100 | 30.6±16.3 |
| Quaking aspen | 4 | 4750±1223.0 | 1.40±0.10 | 69.2±17.00 | 0.17±0.02 | 8.0±1.5 | 0.380±0.050 | 16.3±2.40 | 1.58±0.22 | 75.1±18.2 | 0.310±0.030 | 14.1±3.6 |
| Paper birch | 3 | 5797±3347.0 | 1.50±0.13 | 85.6±8.30 | 0.15±0.01 | 9.0±0.9 | 0.400±0.050 | 23.4±5.50 | 0.99±0.05 | 58.1±9.7 | 0.390±0.050 | 22.8±5.2 |
| Balsam poplar | 3 | 2195±266.0 | 1.29±0.13 | 27.2±5.30 | 0.11±0.01 | 2.2±0.3 | 0.273±0.012 | 4.7 | 2.08±0.06 | 35.6 | 0.410±0.020 | 7.1 |

TABLE 10. Total nutrient pool sizes (grams per square metre) and element concentration in forest floor ($\bar{x} \pm$ SE)

(A) Element concentration

| | | | N | | P | | K | | Ca | | Mg | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vegetation type | $n$ | Biomass | % | Mass | % | Mass | % | Mass | % | Mass | % | Mass |
| Black spruce | 8 | 7646.0±601.9* | 0.83±0.04 | 62.5±5.26 | 0.09±0.01 | 7.3±0.9 | 0.218±0.017 | 17.7±2.34 | 0.33±0.03 | 26.7±3.3 | 0.111±0.014 | 9.1±1.6 |
| All others | 14 | 5191.3±731.3 | 1.24±0.07** | 62.8±6.70 | 0.14±0.01** | 7.3±0.7 | 0.400±0.040** | 22.2±5.40 | 1.40±0.13** | 71.5±11.0** | 0.360±0.030** | 21.2±5.0 |

(B) pH and available nutrient pool sizes in forest floor ($\bar{x} \pm$ SE)

| | | pH | | | K | | Ca | | Mg | | P | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vegetation type | $n$ | 01 | 021 | 022 | g/m$^2$ | mequiv./100 g | g/m$^2$ | mequiv./100 g | g/m$^2$ | mequiv./100 g | g/m$^2$ | mequiv./100 g |
| Black spruce | 8 | 4.50±0.04 | 4.15±0.05 | 4.10±0.12 | 4.26±0.51** | 1.52±0.22** | 14.59±1.85 | 9.18±1.09 | 4.02±0.57 | 4.58±0.80 | 79.6±8.7 | 11.07±0.87 |
| All others | 11 | 5.54±0.08** | 5.99±0.13** | 5.77±0.14** | 1.71±0.37 | 0.84±0.10 | 54.80±7.10* | 44.50±4.11** | 5.85±0.92 | 9.25±0.83** | 176.2±41.4 | 32.68±6.81* |

**, *Difference between means significant at $\alpha = 0.01$ and 0.05.

TABLE 11. pH and exchangeable nutrient pool size and concentration for forest floor ($\bar{x} \pm SE$)

| Vegetation type | $n$ | pH | | | K | | Ca | | Mg | | Available P | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 01 | 021 | 022 | g/m² | mequiv./100 g | g/m² | mequiv./100 g | g/m² | mequiv./100 g | mg/m² | ppm |
| Black spruce | 8 | 4.50±0.04 | 4.15±0.05 | 4.10±0.12 | 4.26±0.51 | 1.52±0.22 | 14.6±1.8 | 9.2±1.1 | 4.02±0.57 | 4.58±0.80 | 79.6±8.7 | 11.07±0.87 |
| White spruce | 4 | 5.43±0.29 | 5.96±0.22 | 5.79±0.16 | 2.62±0.90 | 0.89±0.20 | 56.7±12.9 | 37.6±1.3 | 6.30±1.20 | 6.95±0.12 | 148.8±40.1 | 25.01±10.50 |
| Quaking aspen | 4 | 5.52±0.13 | 5.94±0.13 | 5.70±0.22 | 2.10±0.72 | 1.07±0.16 | 30.0±10.3 | 59.8±7.2 | 6.23±1.89 | 10.76±0.88 | 217.6±102.5 | 42.50±17.00 |
| Paper birch | 3 | 5.55±0.21 | 5.73±0.27 | 5.34±0.13 | 1.17±0.10 | 0.66±0.13 | 41.1±7.7 | 43.9±1.5 | 8.90±1.29 | 12.57±0.54 | 312.4±67.5 | 52.60±5.30 |
| Balsam poplar | 3 | 5.64±0.17 | 6.48±0.22* | | 0.53±0.21 | 0.64±0.27 | 13.5±3.6 | 33.8±12.7 | 1.71±0.37 | 6.96±2.38 | 21.2±9.2 | 9.80±4.10 |

*Combined 021 and 022 horizons.

ecosystems and the absence of moss, a general characteristic of the broadleaved, deciduous forests. Lowest nutrient pool sizes were encountered in poplar, reflecting the smaller forest-floor biomass (Table 9). Among the remaining forest types, black spruce had the lowest reserves of Ca and Mg (Fig. 1). Significantly lower concentrations of all elements were found in black spruce with Ca and Mg concentrations 4 (0.33 vs. 1.40%) and 3 (0.11 vs. 0.36%) times less, respectively, than those encountered in the other vegetation types (Table 9). Only in the case of Ca was the element pool size significantly less in black spruce. The largest Ca (56.7 g/m²) and Mg (8.9 g/m²) reserves were found in white spruce and birch, respectively. The largest pools of N (86 g/m²) and P (9.0 g/m²) were encountered in birch.

Black spruce was found to have the largest exchangeable K pool (4.3 g/m²) but smaller exchangeable Ca (14.6 g/m²) and Mg (4.0 g/m²) pools than encountered in the more productive forest types (Tables 9 and 10). Highest concentrations of available P were found in the latter types.

Black spruce also displayed the greatest cation exchange capacity (CEC), 9.2 equiv./m², indicating that these forest floors may be highly effective in retaining base forming elements. However, these forest floors also were the most acidic (average pH 4.27), and the percentage base element saturation (mequiv./100 g of K + Ca + Mg/CEC, mequiv./100 g) was lowest (15.6%). Hydrogen and probably aluminum are undoubtedly effective competitors for ion-exchange sites in these conditions. In other types, pH ranged from 5.3 in birch to 6.5 in poplar. Base element saturation ranged from approximately 50% in white spruce to between 60 and 62% in the hardwood forest types.

The residence time for biomass and P, K, Ca, and Mg in the forest floor was significantly longer in black spruce than in the other vegetation types (Table 12). Approximately 50 years is required for turnover of black spruce forest-floor organic matter and from 40 (Ca) to 100 (P) years for turnover of the respective elements. These values compare with 15 years for biomass and 20 (Ca) to 40 (N) years for the elements among the more productive ecosystems (Table 12).

*Mineral-soil chemical properties*

In upland ecosystems, largest accumulations of organic carbon are encountered in black spruce soil (Table 13). The average, about 7.3 kg/m², is nearly twice that encountered in white spruce and aspen (4.1 to 4.2 kg/m²) and approximately 1.5 times greater than carbon accumulated in soil of paper birch ecosystems (4.8 kg/m²). Floodplain soil shows the highest average accumulated total carbon (organic plus carbonate carbon), up to 13.5 kg/m² in balsam poplar ecosystems.

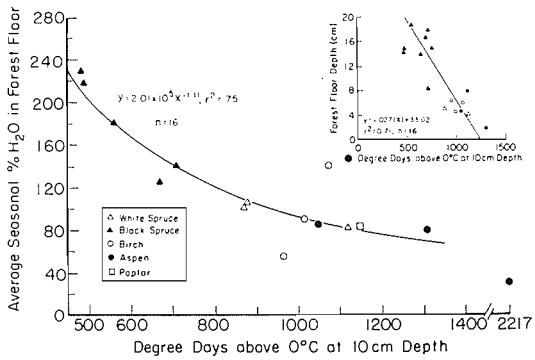


FIG. 2. Average seasonal water concentration and depth of forest floor in relation to soil heat sum (Van Cleve *et al.* 1983).

However, 20 to 60% of the total may be composed of $CO_3C$. The largest amounts of $CO_3$ were measured during the first 100 years of forest development, followed by a gradual reduction in amount through the oldest ecosystems in which soil analysis was conducted (250 to 300 years). Floodplain white spruce soil showed an average of 7 kg/m$^2$ accumulated total carbon. Allowing for the amount of soil carbonate results in an estimate of the average organic carbon of 5.5 kg/m$^2$ in white spruce and 6.8 kg/m$^2$ in balsam poplar. Presence of carbonate in the floodplain soils is associated with neutral to alkaline (pH 7.0 to 8.5) mineral soil pH in contrast to slightly acid (pH 6.5) to strongly acid (pH 4.5) upland mineral soils. On the floodplain, soils supporting balsam poplar generally display neutral to alkaline pH throughout the profile while white spruce soils show slight to strong acidity (pH 4 to 5) in the surface 10 to 20 cm, then a neutral to alkaline subsoil. In the uplands, black spruce displays strongly acid surface mineral soil (pH 4 to 5) in contrast with slightly acid conditions encountered in white spruce, birch, and aspen soils.

Average cation exchange capacity ranged from approximately 60 to 90 equiv./m$^2$ (10 to 20 mequiv./100 g) in upland forest soils (Table 13). Birch and white spruce displayed the highest average CEC, 90 and 77 equiv./m$^2$, respectively. Black spruce and aspen mineral soils occupied an intermediate position with 60 to 65 equiv./m$^2$. The fairly high black spruce mineral soil CEC may reflect high soil organic carbon content. Floodplain white spruce and poplar have approximately 57 and 85 equiv./m$^2$ (5 to 13 mequiv./100 g for white spruce, 6 to 16 mequiv./100 g for poplar) cation exchange capacities, respectively.

Average mineral soil nitrogen content ranged from about 240 g/m$^2$ to slightly more than 400 g/m$^2$ in the uplands. Lowest N pools, 240 g/m$^2$, were encountered in white spruce and aspen. Black spruce and birch showed an average of 307 and 458 g/m$^2$, respectively. Floodplain white spruce and poplar displayed 413 and 587 g/m$^2$ N, respectively. Carbon to nitrogen ratios for upland forest soils ranged from 24 in black spruce to 17 in white spruce and aspen to 11 in birch. Based upon total carbon (including $CO_3$ C) average floodplain soil C/N ratios are 17 for white spruce and 23 for poplar. Based upon preliminary estimates of the organic carbon content, the C/N ratios were 13 and 12 for white spruce and poplar floodplain soil, respectively.

The average upland mineral soil phosphorus pool ranged from approximately 316 g/m$^2$ in white spruce to 574 g/m$^2$ in black spruce. Birch and aspen soil profiles showed an average of about 360 and 465 g/m$^2$ of P, respectively. Floodplain white spruce and poplar mineral soil contained nearly the same amount of P, 480 g/m$^2$. Exchangeable base element concentrations generally were highest in the more productive vegetation types compared with black spruce, regardless of topographic location of the site. The average K, Ca, and Mg pools in black spruce contained 14, 300, and 59 g/m$^2$, respectively. For birch, aspen, and white spruce soils, exchangeable K ranged from 23 to 30 g/m$^2$, exchangeable Ca from 350 to 1409 g/m$^2$, and exchangeable Mg from 65 to 227 g/m$^2$. Largest Ca pool sizes were encountered in floodplain soils, 1140 g/m$^2$ in white spruce and 1409 g/m$^2$ in poplar. Maximum K pool size was found in poplar. Upland white spruce and paper birch mineral soil showed the highest Mg, 227 and 179 g/m$^2$, respectively.

TABLE 12. Residence times (years) for selected elements in forest floor ($\bar{x}$ ± SE)

| | *n* | Biomass | N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|---|
| Black spruce (taiga)[a] | 5 | 50±5 | 61±10 | 99±23 | 74±13 | 39±3 | 73±12 |
| All others (taiga)[a] | 11 | 15±3 | 38±6 | 28±8** | 28±7** | 21±4** | 30±7** |
| Taiga coniferous[a] | 8 | 33±11 | 56±6 | 84±17 | 65±12 | 36±3 | 66±10 |
| Taiga deciduous[a] | 8 | 13±3* | 33±8* | 17±6** | 23±5** | 18±3** | 24±5** |
| Temperate coniferous[b] | 13 | 17 | 18 | 15 | 2 | 6 | 13 |
| Temperate deciduous[b] | 14 | 4 | 6 | 6 | 1 | 3 | 3 |

[a]For biomass only *n* = 8 and 14 for black spruce and other forest types, 13 and 9 for conifer, and deciduous type comparisons.
[b]Temperate coniferous and temperate deciduous estimates from Cole and Rapp (1981).
**, *Difference between means, significant at α = 0.01, 0.05, black spruce vs. all other taiga; taiga coniferous vs. taiga deciduous.

TABLE 13. Selected mineral soil chemical properties[a]

| Vegetation type | $n$ | CEC, equiv./m$^2$ | | Carbon, kg/m$^2$ | | N, g/m$^2$ | | P, g/m$^2$ | | Exchangeable elements | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | K, g/m$^2$ | | Ca, g/m$^2$ | | Mg, g/m$^2$ | |
| | | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ | Range | $\bar{x}$ |
| Black spruce | 6 | 11–136 | 65 | 4.1–10.4 | 7.3 | 192–406 | 307 | 85–1642 | 574 | 1.3–31.0 | 13.9 | 64–548 | 304 | 13.3–135.6 | 58.6 |
| White spruce F | 4 | 39–84 | 57 | 3.8–10.6 | 7.2 | 220–614 | 413 | 446–517 | 483 | 10.2–49.3 | 22.7 | 350–1857 | 1142 | 0.5–2.2 | 93.2 |
| White spruce U | 3 | 71–88 | 77 | 3.0–5.8 | 4.1 | 201–298 | 242 | 205–386 | 316 | 30.2–34.7 | 32.5 | 457–730 | 594 | 222.0–232.0 | 227.0 |
| Quaking aspen | 2 | 57–61 | 59 | 3.6–4.9 | 4.2 | 194–307 | 241 | 308–555 | 465 | 13.7–58.2 | 32.9 | 272–477 | 352 | 75.5–78.4 | 77.0 |
| Paper birch | 2 | 85–95 | 90 | 3.9–5.7 | 4.8 | 400–516 | 458 | 263–460 | 362 | 12.0–45.3 | 28.5 | 182–767 | 475 | 126.6–232.2 | 179.4 |
| Balsam poplar | 3 | 65–98 | 85 | 9.3–18.1 | 13.5 | 453–820 | 587 | 444–506 | 484 | 21.6–49.3 | 36.1 | 881–1759 | 1409 | 48.9–85.6 | 65.2 |

NOTE: F, floodplain soil; U, upland soil.
[a]For 70 cm profile depth or to permafrost table (black spruce), or bed rock in upland forest types if at shallower depth. See Viereck *et al.* (1983) for profile descriptions.

*Controls of productivity and nutrient cycling*

Black spruce ecosystems occupy sites which display the coldest soil temperatures (Fig. 2). Average seasonal soil heat sums for all other forest types (1132 ± 92 DD) were significantly higher ($P = 0.01$, $n = 22$) than those encountered for black spruce (640 ± 40 DD). This condition is strongly related to forest-floor thickness (Fig. 2). Significantly more biomass accumulates in thicker layers ($P = 0.01$, $n = 22$) in black spruce ecosystems. The average forest-floor thickness, 15 cm, is nearly 3 times the average of 6 cm encountered in the other forest types. In addition to cool soil temperatures, highest average seasonal forest-floor and mineral-soil moisture contents are encountered in black spruce (Fig. 2). Conclusively, black spruce occupies sites which display the coldest, wettest forest floors and mineral soils.

Low soil temperature translates to the smallest accumulation of tree biomass, standing crop of elements, annual production, and element requirement in aboveground tree components (Fig. 3). Moreover, biomass and element return in overstory litter fall in black spruce is the lowest and turnover of biomass and elements is slowest in the forest floor. Across the range of vegetation types examined in this study the annual tree biomass production and element requirement is significantly related to soil temperature (Fig. 3). For these regressions $R^2$ ranged from about 0.79 for K requirement to 0.90 for production. In each case black spruce occupies the lower end of the curves, displaying the lowest production and element requirements of any of the forest types.

Interacting with soil temperature to control productivity and nutrient cycling is forest-floor chemistry (organic matter quality). Previous discussion emphasized the reduced concentration of elements encountered in black spruce forest floors. In addition, this vegetation type has the highest forest-floor lignin concentration. Lower concentration of elements (including energy supplies) important to microbial activity but higher concentration of decay resistant materials (lignin) interact with soil temperature to reduce forest-floor decomposition and element recycling (Fogel and Cromack 1977; Aber and Melillo 1980; Sharpe *et al.* 1980; Moore 1981; Flanagan and Van Cleve 1983). This condition is illustrated in similar average total pool sizes of N, P, and K in the forest floor of black spruce and the other forest types (Table 10A), but significantly longer element residence times in black spruce forest floors (Table 12).

Forest-floor C/N and C/P ratios may also be related to the recycling of N and P for tree use (Alexander 1977). Soil ratios larger than 20 or 30 for C/N generally indicate a potential for microbial immobilization of N. Ratios larger than 100 or 300 for C/P may indicate

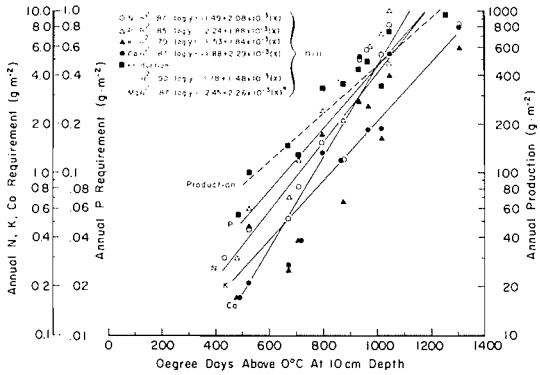


FIG. 3. Relationship between soil heat sum and annual requirement by aboveground tree components for N, P, K, Ca, and net annual aboveground tree production.

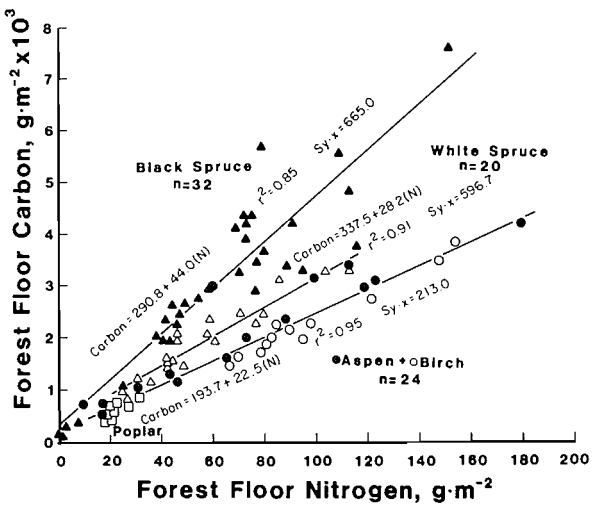


FIG. 4. Carbon in relation to nitrogen in forest floor of principal taiga forest types.

potential for microbial immobilization of P. Both ratios are significantly larger in black spruce compared with the other forest types ($P = 0.01$). For white spruce and the hardwood types the C/N ratio ranges between 28 and 23 (Fig. 4) while the C/P ratio ranges between 250 and 240 (Fig. 5). On the other hand, black spruce shows a C/N ratio of 44 and a C/P ratio of 404 (Fig. 5). Both ratios are significantly related to annual tree requirement for N ($R^2 = 0.75$) and P ($R^2 = 0.51$) and the C/N to annual production ($R^2 = 0.69$, Figs. 6 and 7).

In Figs. 8 and 9 the ratio of biomass (B) to N and P for litter fall and the forest floor was employed as an analog of the C/N and C/P ratios because carbon analysis was not available for litter fall samples. These relationships demonstrate that forest types developing on substrates of low quality and in which the recycling of N and P potentially is limited (such as the case of

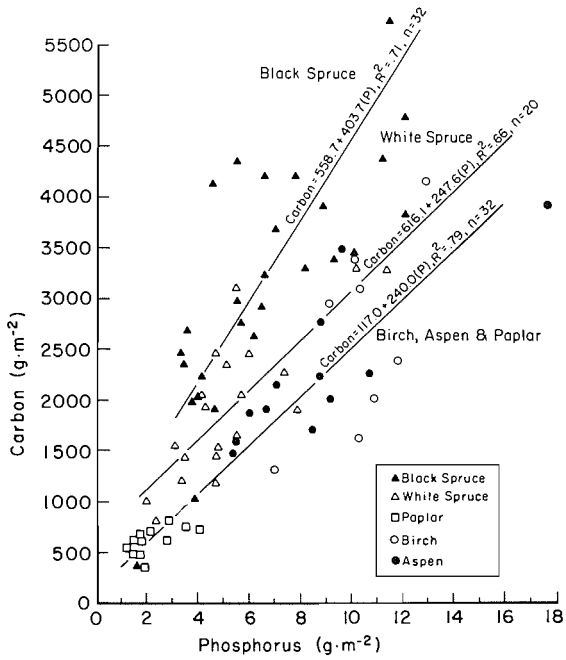


FIG. 5. Carbon in relation to phosphorus in forest floor of principal taiga forest types.

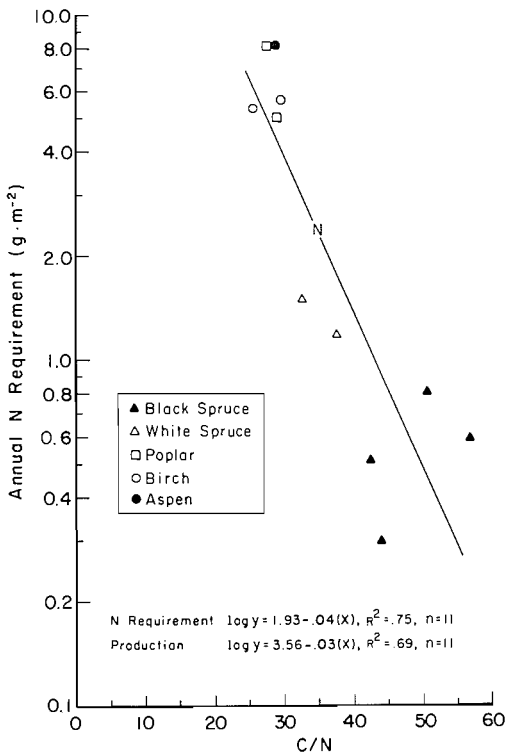


FIG. 6. Annual aboveground tree N requirement compared with forest floor C/N ratio.

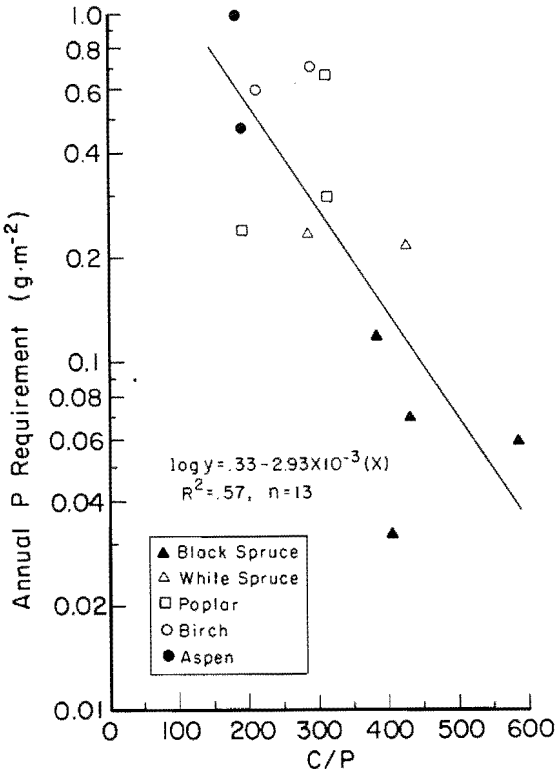


FIG. 7. Annual aboveground tree P requirement compared with forest floor C/P ratio.

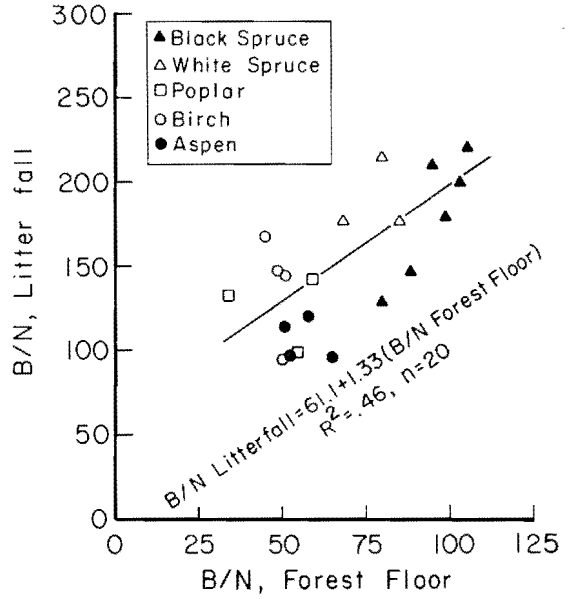


FIG. 8. Biomass/N ratio of litter fall compared with biomass/N ratio of forest floor.

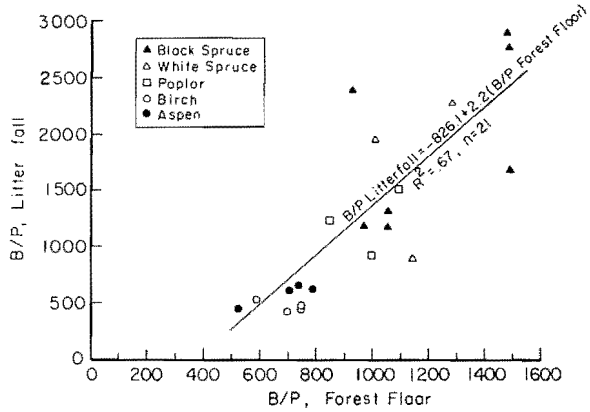


FIG. 9. Biomass/P ratio of litter fall compared with biomass/P ratio of forest floor.

black spruce) will recycle organic matter which also is of low nutrient content. This condition reinforces the development of low tree productivity. Organic matter from which N and P may more rapidly be recycled generally is produced by the hardwood forest types. This rate of nutrient cycling supports greater forest tree productivity. Similar relationships were demonstrated for sites in the contiguous 48 states by Vitousek *et al.* (1982). In this case the percentage of N mineralized in 8-week, aerobic laboratory incubations of the forest floor was greater for sites which displayed larger amounts of N recycled in litter fall. Moreover, across a broad latitudinal range of forest sites these authors found decreasing litter fall C/N ratio associated with increasing litter fall N.

The question of dominant environmental control or controls with regard to ecosystem structure and function is difficult to establish. Correlation analysis of system processes on the basis of field data may not clearly separate interaction among independent variables. An example is the difficulty in separation of the temperature–moisture control from forest-floor chemistry (quality) control with regard to decomposition processes, nutrient cycling, and tree growth. Two experiments were conducted which separately examined the influence of soil temperature and forest-floor organic matter quality on organic matter decomposition and nutrient supply for plant growth. In the first experiment, heating of about 400 $m^2$ of black spruce forest floor to approximately 9°C above ambient temperature for three summers resulted in a 20% reduction in forest-floor biomass (8360 to 6488 $g/m^2$). During this period the 022 horizon (H-layer) showed a significant ($\alpha$ = 0.05) decline in weight of 742 $g/m^2$. This weight change was associated with significant ($\alpha$ = 0.05) increases in exchangeable $NH_4$ and available P in the forest floor and in Kjeldahl nitrogen in soil solution. As a result of the more favorable nutrient and temperature regimes, spruce foliage showed increased rates and

TABLE 14. Average (±SE) estimates for element cycling in coniferous and deciduous forest types (grams per square metre per year)

| | *n* | Process | N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|---|
| Coniferous | 6 | Uptake | 0.76±0.18 | 0.09±0.03 | 0.50±0.20 | 1.30±0.47 | 0.14±0.06 |
| | 8 | Requirement | 1.04±0.29 | 0.13±0.03 | 0.86±0.28 | 0.81±0.23 | 0.15±0.04 |
| | 6 | Return | 0.49±0.13 | 0.05±0.02 | 0.27±0.12 | 1.03±0.40 | 0.09±0.04 |
| Deciduous | 7 | Uptake | 2.23±0.36** | 0.47±0.08** | 1.74±0.32** | 6.29±1.55* | 0.95±0.17** |
| | 8 | Requirement | 5.85±0.71** | 0.61±0.09** | 2.89±0.36** | 3.83±0.81** | 0.97±0.13** |
| | 7 | Return | 2.51±0.58** | 0.38±0.07** | 1.30±0.26** | 5.55±1.40* | 0.81±0.15** |

*, ** means within ecosystem process significantly different between forest types at $\alpha = 0.05, 0.01$, respectively.

photosynthesis and significantly higher ($\alpha = 0.05$) concentrations of N (1.05% heated vs. 0.76% control), P (0.14% heated vs. 10% control), and K (0.80% heated vs. 0.56% control) compared with untreated trees. The results of this experiment showed the influence of forest-floor temperature on microbial control of organic matter decomposition and release of nutrient elements for tree use.

In the second experiment forest floors from representative stands of six of the principal forest types were tested for ability to supply N for paper birch seedling growth. The forest types included alder (*Alnus incana*), birch, aspen, poplar, white spruce, and black spruce. Organic material was uniformly mixed with sand. The potted mixtures (four replicates per type) were planted to birch seedlings (three seedlings per pot) and supplied weekly with a complete nutrient solution minus nitrogen. Sufficient deionized water was added to the pots on other days to maintain sand cultures at a saturated but not waterlogged moisture level. Temperature (20°C) and lighting regime (21-h photoperiod) were constant for the experiment. Chemical analyses for C and N were conducted using procedures described earlier in this paper. This bioassay showed strong negative exponential relationships between initial forest-floor C/N ratios and average total seedling yield ($R^2$ = 0.96). Similar strong relationships also existed between the C/N ratios and average seedling mass of total N and mass of seedling root N ($R^2$ = 0.96 and 0.99, respectively). A further comparison between average percent N content in seedling leaf, stem, and root tissue and forest-floor C/N ratios showed the same general relationship ($R^2$ = 0.80, 0.94, and 0.75, respectively). Forest-floor C/N ratios ranged from greater than 50 in black spruce to 20 in alder. While other organic chemical properties of the forest floors cannot be ruled out as contributing to the overall effect, in the case of this experiment the C/N ratio reflected the capacity of different forest floors to supply N for plant use even when soil temperature, moisture, and nutrient regimes (with the exception of N) were favorable for plant growth.

Future research will have to clearly establish the relationship between forest-floor chemistry and the supply of elements for tree growth. Nevertheless it appears that soil temperature and organic matter chemistry are closely related to tree growth and element cycling in these taiga forests (Flanagan and Van Cleve 1983). Especially in the case of black spruce these factors combine to restrict tree growth and nutrient dynamics to the lowest of any forest type in the region.

An additional control of nutrient cycling which is of substantial importance is the deciduous (hardwood) or coniferous morphology of the forest types. This control transcends that of temperature or forest-floor organic matter quality and reflects genetic control of tree growth and element requirement. Earlier discussion emphasized the significantly greater efficiency of element use and reduced average annual element requirement in white and black spruce (Table 4). On the average, deciduous types translocate substantially more N (62% or 3.6 g/m$^2$) from old tissue in support of new tissue production than do the conifers (27% or 0.3 g/m$^2$, Table 14).

Cole and Rapp (1981) found about equal uptake and requirement for N in coniferous types but about one-third of new tissue N requirement in deciduous types was provided by translocation from older tissue. For P, these authors found 14% of requirement met by translocation in deciduous types while uptake exceeded requirement by 70% in coniferous types. In our studies, on the other hand, approximately 80% of the P requirement for new tissue in conifers is provided by translocation compared with only 20% in the deciduous species. Approximately the same portion of K requirement, 40%, is met by translocation in both species groups. Cole and Rapp (1981) found little K translocation in either species group. There is very little translocation of Mg in either deciduous or coniferous types (Table 14). In the case of both types, Ca uptake exceeds demand by a little less than twofold, a result similar to that reported by Cole and Rapp (1981). This condition largely reflects Ca immobility within the tree. In coniferous stands the flux of Ca in throughfall is about 25% of that in litter fall. In deciduous stands, combined throughfall and stemflow are less than 10% of the Ca flux in litter fall. The generally smaller ele-

TABLE 15. Linear correlations between net annual aboveground production and selected indices of cycling for N, P, K, Ca, and Mg in deciduous compared with coniferous forest types

| | | Deciduous | | | | Coniferous | | | |
|---|---|---|---|---|---|---|---|---|---|
| Element | Process | $n$ | $R^2$ | $a$ | $b$ | $n$ | $R^2$ | $a$ | $b$ |
| N | Uptake | 6 | 0 | 538.3 | −4.0 | 6 | 0.99 | −13.9 | 270.6* |
| | Requirement | 8 | 0.86 | −132.0 | 114.2 | 8 | 0.88 | 2.0 | 236.8** |
| | Return | 7 | 0.07 | 407.4 | 43.6 | 6 | 0.97 | −3.6 | 389.5 |
| P | Uptake | 7 | 0.35 | 171.8 | 361.7 | 6 | 0.90 | 49.5 | 1524.5 |
| | Requirement | 8 | 0.38 | 191.8 | 548.5 | 8 | 0.91 | 29.5 | 1327.9** |
| | Return | 7 | 0.18 | 307.2 | 550.6 | 6 | 0.83 | 77.0 | 2281.8 |
| K | Uptake | 7 | 0.61 | 116.7 | 229.7 | 6 | 0.92 | 68.2 | 243.5 |
| | Requirement | 8 | 0.85 | −76.7 | 207.9 | 8 | 0.65 | 81.8 | 168.6 |
| | Return | 7 | 0.49 | 186.7 | 253.2 | 6 | 0.98 | 72.3 | 417.7 |
| Ca | Uptake | 7 | 0.29 | 312.9 | 32.4 | 6 | 0.99 | 51.2 | 106.3 |
| | Requirement | 8 | 0.51 | 245.3 | 72.6 | 8 | 0.96 | 53.1 | 226.7** |
| | Return | 7 | 0.19 | 382.1 | 86.9 | 6 | 0.96 | 57.1 | 125.3 |
| Mg | Uptake | 7 | 0.39 | 192.4 | 339.9 | 6 | 0.88 | 73.5 | 838.4 |
| | Requirement | 8 | 0.55 | 58.8 | 478.0 | 8 | 0.99 | 21.6 | 1365.0** |
| | Return | 7 | 0.28 | 247.1 | 332.3 | 6 | 0.82 | 85.1 | 1144.3 |

NOTE: $n$, number of stands in each forest type used in comparison; $a$, intercept; $b$, slope.
*, **, slope of regression lines for deciduous versus coniferous forest types significantly different at $\alpha = 0.05$, 0.01, respectively.

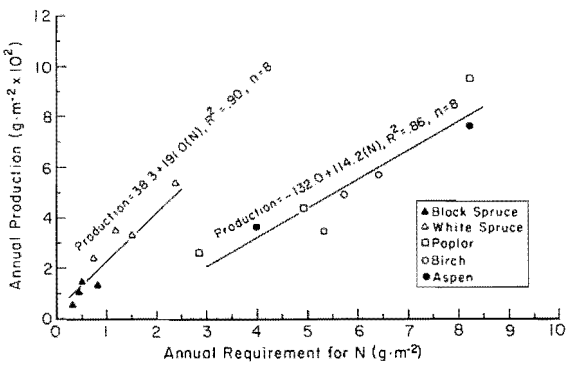


FIG. 10. Annual production in relation to annual N requirement for aboveground tree components.

ment fluxes encountered in taiga ecosystems primarily reflect reduced annual tree production.

In general, stronger correlations were encountered between annual tree production and indices of element cycling for all elements in the coniferous forest types (Table 15, Fig. 10). These correlations reflect the greater efficiency of element use by conifers. They also reflect a reduced turnover of element supplies in coniferous forest floors compared with that in the deciduous types. Element residence times may generally be ranked as black spruce > white spruce > deciduous types (Table 12). For nitrogen, the average residence times are 61, 50, and 33 years, respectively. White spruce ecosystems generally are characterized by cooler soils and greater accumulated forest-floor biomass than encountered in the deciduous types, but not the extreme conditions for these variables encountered in black spruce. White spruce also shows an intermediate annual tree production and element requirement but largest standing crop of biomass and elements. These conditions reflect the adaptation of white spruce to later successional soil environment (Van Cleve and Viereck 1981). In contrast, the deciduous forest types show relatively rapid forest-floor element turnover and hence may generally not be limited to the same degree for element supplies except in the case of N and K. Field-fertilization trials in aspen and birch have consistently shown growth response to N but not P and K (Van Cleve and Oliver 1982; data on file at the Forest Soils Laboratory, University of Alaska, Fairbanks). As pointed out by F. S. Chapin *et al.*,[3] these relationships reflect the adaptation of the slower growing coniferous species and especially black spruce to sites where element supplies are restricted, primarily by interaction of soil temperature and forest-floor chemistry.

*Comparison with temperate forest regions*

Several indices of ecosystem functions were evaluated among geographic regions. Residence time for forest-floor organic matter and selected elements generally is substantially greater for taiga compared with temperate latitude forest types (Table 12). The values range from 2 to 3 times longer for biomass in coniferous

[3]Chapin, F. S., III, P. R. Tyron, and K. Van Cleve. Influence of phosphorus supply on the growth and biomass allocation of Alaskan taiga tree seedling.

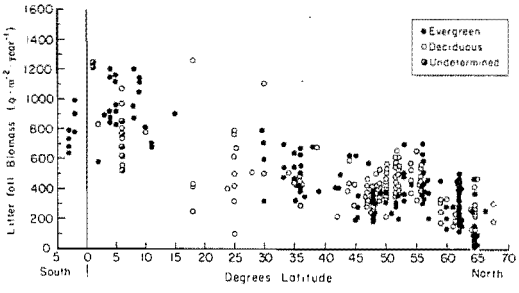


FIG. 11. Forest litter-fall biomass in relation to latitude. Data were abstracted from the following references: Bray and Gorham (1964), Bringmark (1977), Cragg *et al.* (1977), Lousier and Parkinson (1976), Malkonen (1977), Nihlgård and Lindgren (1977), Rodin and Bazilevich (1965), Van Cleve and Noonan (1975), Cole and Rapp (1981), Vitousek (1983), DeAngelis *et al.* (1981).

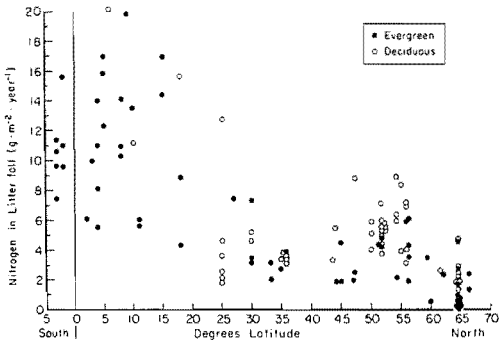


FIG. 12. Mass of nitrogen in forest litter fall in relation to latitude. Data were abstracted from the following references: Bray and Gorham (1964), Bringmark (1977), Cragg *et al.* (1977), Lousier and Parkinson (1976), Malkonen (1977), Nihlgård and Lindgren (1977), Rodin and Bazilevich (1965), Van Cleve and Noonan (1975), Cole and Rapp (1981), Vitousek (1983), DeAngelis *et al.* (1981).

and deciduous types, respectively. Between 20- and 30-fold longer residence times are encountered for K with other elements showing from three to eightfold longer turnover for the taiga forest floors.

Annual litter-fall biomass generally appears to increase with decreasing latitude from 70° to 0° N (O'Neill and DeAngelis 1981). An average in excess of 1100 $g \cdot m^{-2} \cdot year^{-1}$ was estimated at 0° N, the equator. However, the majority of their data also comes from forests north of 35° N. Including the data of Vitousek (1983) and other workers (Fig. 11) the average maximum litter fall, encountered between 10° N and 5° S, appears to range between 900 and 1000 $g/m^2$. The data employed from Vitousek's (1983) summary included only those stands located under 300 m in elevation and greater than 25 years in age. Average taiga litter-fall biomass appears to be about 100 to 200 $g/m^2$ annually

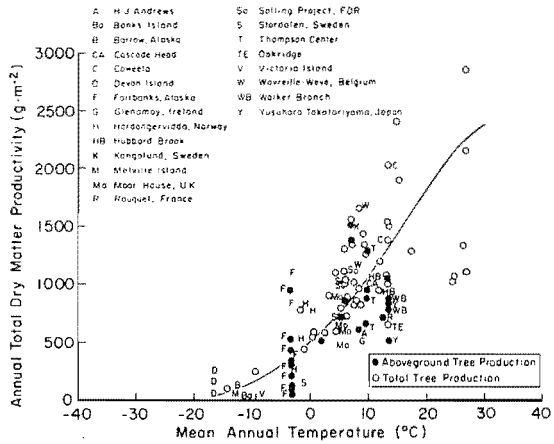


FIG. 13. Annual total dry matter production in relation to mean annual temperature. Data for this figure were abstracted from the following references: Van Cleve and Alexander (1981), Cole and Rapp (1981), Leith (1975).

with a minimum less than 50 $g/m^2$ and a maximum approaching 500 $g/m^2$.

The mass of nitrogen returned in litter fall increases with decreasing latitude to a maximum average between 14 and 16 $g/m^2$ between 10° N and 5° S. Maximum values approach 20 $g/m^2$ (Fig. 12). The same criteria for inclusion of litter-fall biomass data from Vitousek (1983) was employed in using his litter-fall N data. Average annual return of N in taiga forest litter fall appears to lie between 1 and 2 $g/m^2$, 16 to 40% of the average maximum (5 to 6 $g/m^2$) encountered in temperate latitude forests. The substantial scatter in the latitudinal trends of litter-fall biomass and mass of N in litter fall undoubtedly reflects the range of state factors encompassed by various sampling sites including differences in stand age-class and forest stocking and basal area.

Compared with the best temperate latitude forests, annual tree dry matter production in taiga forests appears to range from about 3% in low productivity black spruce, to 50% in productive balsam poplar, of literature values (Fig. 13). However, the most productive white spruce stands, located along the Yukon River north of Fairbanks, may annually produce aboveground 2500 $g/m^2$ of dry matter (Yarie and Van Cleve 1983). This exceeds total net tree production (tops and roots) of some temperate latitude pine plantations (2000 $g/m^2$, Cole and Rapp 1981).

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gram, and the Institute of Northern Forestry, United States Forest Service.

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